

Female Mate Choice in a Lek Mating System: Assessing Behavioral Correlates of Mating Success

By

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Abstract

A central aspect in the study of sexual selection is to understand the process whereby some individuals gain an advantage over conspecifics of the same sex in terms of reproduction. Sexual selection often occurs through intra-sexual competition for access to females and via inter-sexual choice of opposite sex traits. The aim of this study was to understand female mate choice in the Blue-backed Manakin (Aves, Pipridae, *Chiroxiphia pareola*) by examining the association between male behavioral traits and reproductive success. As a first step we described aspects of the natural history of a color-banded population in Amazonian Ecuador. Display areas consisted of 1-6 dance perches occupied by 1-5 males with ages ranging from 4+ years to 16+ years. Male *C. pareola* had a repertoire of at least six different vocalizations, including invitation calls, duet vocalizations and display vocalizations; dance displays consisted of solo dances

and two-male dance displays. We detected a bimodal pattern of perch and vocal activity, with peaks early in the morning and in the afternoon. We then evaluated correlates of male mating success by examining associations between number of female visits to the display areas and male display area attendance, vocalization and display activity. We hypothesized that males that invest more in display activities would be preferentially selected by females. We found that male display area attendance, two-male display duration for females and vocalization activity at display areas were positively and highly correlated with the number of female visits. Our results also suggest that cooperative display behavior is important to achieve a high reproductive success; variables indicating cooperation between two-male or groups of males, were significantly correlated with the number of female visits. In sum our results suggest that behaviors signaling vigor are important targets of sexual selection in our study species.

Key words: Female mate choice, Manakins, displays, camera traps, *Chiroxiphia*, vocalizations.

Introduction

Sexual selection refers to the process whereby some individuals gain an advantage over conspecifics of the same sex exclusively related to reproduction (Darwin 1871). A central aspect in the study of sexual selection is to understand which traits allow individuals to achieve greater mating success (Bradbury & Andersson 1986).

Sexual selection often occurs through intra-sexual competition for access to females and via inter-sexual choice of traits exhibited by the opposite sex (Darwin 1871). Despite having been extensively studied, female mate preferences remain difficult to explain. From a theoretical point of view, many hypotheses that account for female preferences have been proposed including females acquiring direct benefits for themselves or their offspring (e.g. territory, food, parental care; Emlen & Oring 1977, Bradbury & Andersson 1986), or indirect benefits when males provide no resources for females or offspring (Kirkpatrick & Ryan 1991). When females gain only indirect benefits, female preferences are expected to drive the evolution of male traits via a runaway process (i.e., the 'sexy sons' hypothesis Kirkpatrick 1982, Lande 1981) or via their selection of 'good genes' (Zahavi 1975, Hamilton & Zuk 1982).

The runaway sexual selection hypothesis (Fisher 1930) assumes genetic variation in female sexual preferences and that, being heritable, such preferences can evolve. Female preferences are expected to exert selection on male traits, which may result in the exaggerated development of secondary sexual characters, especially if alleles associated with female preferences are genetically linked to these encoding male traits. Under this model, sons of “choosy” females will inherit attractive traits from their fathers and will have more reproductive success because they will, in turn, be chosen by selective females. Consequently, female preferences for exaggerated male traits can become fixed, even if such traits do not confer greater viability to the offspring (Kirkpatrick 1982, Lande 1981, Kirkpatrick & Ryan 1991, Kokko 2003).

The ‘good genes’ hypothesis (Hamilton & Zuk 1982) poses that male secondary sexual characters (which may be morphological, physiological or behavioral) correlate with variation in genes enhancing viability. Thus, females may use these traits as honest indicators of individual quality. By mating with a vigorous male, a female gains an evolutionary advantage by passing his ‘good genes’ on to her offspring. If female selection of good genes increases offspring fitness, then female preferences will be reinforced, and exaggerated development of male traits will follow (Hamilton & Zuk 1982, Kirkpatrick & Ryan 1991, Andersson 1994). Because females select males of overall better quality, one does not expect among-female variability in preferences under this model.

Many studies on sexual selection in birds have evaluated female mate choice and its consequences for reproductive success. Regardless of the mechanisms through which female preferences have evolved, sexual selection resulting from female mate choice based on particular male characteristics implies that male individuals will vary considerably in reproductive success, resulting in marked reproductive skew. Most of these studies have been conducted on species forming classical leks in which females can choose to mate with any male that holds a display arena within the lek. Mate choice in these systems likely differs from that in species forming exploded leks (i.e., where arena-holding males are within hearing distance from one another but not in visual contact); in some of these exploded leks multiple males occur within a single display arena and dominance hierarchies exist within these arenas. In these latter lek-breeding systems, female mate choice is limited to choosing only between the dominant males at

each arena forming a lek, which likely results in strong reproductive skew (McDonald 1989b, Duval & Kampenaers 2008).

Most studies on mate selection in lekking species have focused on evaluating the influence of traits associated to characteristics of the territory and ornaments or other morphological characteristics of males. Fewer studies have attempted to evaluate female mate choice based on behavioral traits that indicate male vigor (e.g. the frequency with which males perform costly displays), probably due to the difficulty in obtaining such data. Energetically costly behavioral traits are likely honest indicators of male quality because, in contrast to some types of ornaments, vigor can hardly be faked (i.e., it cannot be decoupled from overall performance; Byers et al. 2010). Therefore, if females use behavioral traits related to vigor as cues to choose their mates, then they are likely to choose 'good genes' for their progeny.

An appropriate system to study female preferences for male characteristics associated with vigor and resulting in high reproductive skew are birds in the family Pipridae (manakins). Manakins are frugivorous birds exhibiting sexual dimorphism and elaborate male courtship displays. Males aggregate in display arenas or leks for the sole purpose of attracting and courting females (Emlen & Oring 1977, Davis 1982, Foster 1977, 1981, 1987, Prum 1994, 1997). Females visit male arenas only to copulate, and then build nests and rear offspring without any assistance from the male; thus, males do not provide any direct benefit for the female or her offspring. All this results in intense sexual selection (Skutch 1949, Foster 1976, 1983, Emlen & Oring 1977, Snow 2004). Because males provide no direct benefits to females, male traits (including courtship behavior) are likely the only cues females have to assess male quality prior to mating.

Species in the genus *Chiroxiphia* exhibit cooperative behaviors, where groups of males perform coordinated displays at fixed display perches in their areas to attract females (Gilliard 1959, Snow 1956, 1963, 1971, Foster 1981, 1977). There is a dominant alpha male at each display area, which is typically the only one that copulates with females (in exceptional cases beta males can get copulations; Foster 1983, McDonald 1989a, Duval & Kampenaers 2008). For some species, only a few alpha males may be responsible for siring 80-90% of the offspring (McDonald 1989a, 1989b). However, part of the success of the alpha male depends on its cooperation with beta males (McDonald 1989a, 1989b, Trainer & McDonald 1993, DuVal & Kampenaers 2008, 2012). This seems paradoxical

given the intense sexual selection, high reproductive skew, and low rate of agonistic interactions reported for some species of the genus.

The aim of this study was to evaluate female mate choice in a system with high reproductive skew, where males are organized in display arenas with a hierarchical structure and cooperate with seemingly no agonistic encounters. We examined the association between male behavioral traits and reproductive success (i.e. female visits), and assessed the influence of cooperation between males in helping alpha males to achieve reproductive success in the Blue-backed Manakin (*Chiroxiphia pareola*). In contrast to similar studies conducted previously which conducted behavioral observations at leks (McDonald 1989, Shorey 2002, Duraes 2009), we combined the use of focal observations with innovative sampling techniques based on camera traps and automated audio-recording devices that enabled us to intensively sample male behavior and female visitation at leks over continuous periods.

As a first step to evaluate variables associated with female mate choice in the Blue-backed Manakin, we described the display areas, the seasonal and daily patterns of activity at display areas, the social organization, the vocalization repertoire and the display behavior of a color-banded population in Amazonian Ecuador (Loiselle et al. 2006, 2007). This population corresponds to the previously unstudied subspecies *C. p. napensis*. We then evaluated correlates of male mating success by examining associations between the number and duration of female visits to the display area with male display area attendance, vocalization activity, display activity, number of individuals associated to the display area, and estimates of age of the alpha male. We hypothesized that males that invest more in display activities will be preferentially selected by females.

Methods

1. Study system

The Blue-backed Manakin is one of the largest species in the Pipridae (adult males weigh 20-25 g). Adult males are black with a red cap and a sky-blue patch on the upper back; females and first-year males are olive green (Snow 1963, Ridgely & Tudor 1994).

As with other species in the genus (DuVal 2005, McDonald 1989a), males exhibit delayed plumage maturation, reaching full adult plumage in their fourth year (B.A. Loiselle, unpubl. data). The structure of display areas in the Blue-backed Manakin is hierarchical, consisting of one alpha male, one beta male, and several gamma males of different ages and stages of plumage maturation (Snow 1963, 1971). The species comprises four subspecies inhabiting wet lowland forests (500-1700 m elevation) of Trinidad and Tobago; the Guyanas; eastern Venezuela, Ecuador, Colombia, and Peru; and Amazonian Brazil (Clements version 6.8 2013, Ridgely & Tudor 1994).

2. *Study site*

We studied Blue-backed Manakin at Tiputini Biodiversity Station (TBS), a 650-ha area of lowland wet forest located in Orellana province, Amazonian Ecuador ($\sim 0^{\circ} 38' S$, $76^{\circ} 08' W$); TBS is located within the Yasuni Biosphere Reserve, which encompasses ~ 1.7 million ha of lowland wet forest. TBS has approximately 30 km of trails and two 100-ha plots (Harpia and Puma) where several studies on behavioral ecology and sexual selection in lekking manakins have been conducted for more than 10 years (Blake & Loiselle 2002, 2008, Loiselle et al., 2006, 2007, Durães et al. 2009, 2011, Ryder et al. 2009a, 2009b, Hidalgo et al., 2008). We focused our study within and nearby these plots; field work was conducted in January-March 2013 at TBS, which corresponds to part of the breeding season (Durães et al. 2011).

3. *General field methods*

We focused sampling effort on seven display areas of which four were located in the Harpia plot, one in the Puma plot, one near the Chorongó trail and one adjacent to the Parahuaco trail (Fig. 1). These display areas were previously identified, mapped and characterized (Loiselle et al. 2007), and most of the males were banded with a unique combination of three color-bands and a numbered aluminum-band. Information on the age and status of each banded male has been recorded yearly for over 10 years.

We visited each display area for periods of 2 hours from 0630 hours to 1800 hours and made focal observations to identify individuals and count the number of males

associated with each area. For males that were banded and which we associated to a display area, minimum age was calculated using historical information (B. A. Loiselle, unpublished data). Given that male Blue-backed Manakins experience a 4-year plumage maturation process, ages were calculated according to the plumage of the bird during the first year of capture. In their hatch-year males are olive green, the second year they grow a red cap, during the third year the blue patch on the back appears and some black feathers in the body, and in the fourth year they reach full adult plumage (B.A. Loiselle, unpublished data, DuVal 2005). Thus, if a bird was in adult plumage in the first year of capture an age of 4+ years was assigned and minimum age in the observation year was estimated based on the date of first capture.

Unbanded males were captured using mist nets and banded at the end of the field season. In an effort to record most of the displays and behaviors, we identified at least two primary dance perches for each display area, and GPS points were taken for every display area and every dance perch. Dance perches were identified using by following the vocalization uttered by males during cooperative dance displays. Male Blue-backed Manakin within an display area can use 4-6 dance perches, although they concentrate most activity on a couple of dance perches.

Every time a dance perch was identified, we marked a nearby shrub (i.e. 4-5 m distant) with flagging tape that indicated the orientation, distance from the observer, height of the perch, band color combination (when possible), date, and age class and behavior (e.g., singing or not) of the bird. We then located a camouflaged camera trap (PC800 HyperFire Professional Semi-Covert IR, by Reconyx) within 1-2 m from the dance perch at each display area to continuously record male visits, displays, and female visits and copulations. Cameras were set to take photos every 5 seconds between 0630 hours and 1630 hours to capture the time manakins were potentially active on the dance perch. In total, we sampled for 5,330 camera hours, obtaining a total of 11,836 photos (Table 1). Most photos were monochromatic, except when enough sunlight reached the camera.

To record vocal activity at each display area, we used automatic vocalization recorders (Songmeter SM2+, by Wildlife acoustics 2010) with two omni-directional microphones (SMX-II Weatherproof Acoustic Microphone). Each microphone was attached to the recording box using a 10-m cable placed near one of the two primary dance perches. Songmeters were programmed to record stereo at a sampling rate of 16 kHz in *.wav

format. We recorded continuously for one-hour cycles during ten hours per day, from 0630 hours to 1630 hours for periods of 7 days, between the last week of January until the third week of February. A total of 1865 hours of recordings were obtained but only 730 were analyzed (Table 1).

Display dances were also recorded using video cameras (HX-WA2 HD Camcorder, Panasonic). Cameras were mounted on a stake within 1-2 m from the dance perch and programmed to record for periods of two hours at a time. A total of ~133 hours were recorded obtaining only 36 minutes of perch visits and display dances.

4. Activity Patterns at Display areas

To describe the daily activity of manakins on their dance perches we set cameras to record date, time and ambient temperature when photos of birds were taken. To measure display area attendance we registered the total number and duration of male visits per day. We defined a male visit as an instance when a male was sitting on the dance perch, calling from the perch or cleaning it. To measure the time devoted to cooperative dance displays we registered the total number and duration of two- male dance displays per day, separating them by whether they were performed with or without female presence. The absence or presence of females differentiates whether two-male dance displays were practice bouts by males associated to the display area or performance bouts by males directed towards females, respectively. To quantify alpha male performance we used pre-copulatory displays (see below in dance display description) and registered total number and duration of single male displays per day with and without female presence (again to separate instances of single males practicing) (Table 2).

The duration of visits and dance displays was calculated counting the time elapsed between the shooting of the first photo where the bird appeared or a display behavior was observed until the shooting of the last photo in which the bird was on the perch or displaying. A visit was considered to have ended when males abandoned the dance perch for more than 60 seconds. We combined data from different dance perches within a display area for each date and all variables were corrected by number of hours sampled per date for analyses. Information on sex, age and color-band combination of the individuals visiting the perches was collected from the photos when possible.

To characterize the vocal activity of Blue-backed Manakin we analyzed recordings using the software SongScope (Wildlife acoustics, Inc 2010) and Adobe Audition 1.5 (Adobe Systems Incorporated, 2004). We examined spectrograms of all the recording files obtained for all display areas in Audition to assess recording quality and to filter out problematic files (e.g. those in which microphones did not function properly or those in which rain did not allow adequate recording). Using SongScope we built a song-recognition model (Recognizer) to search for and automatically identify the most common vocalization for the Blue-backed Manakin (a “*pchrrr*”, see below) across all the files. To create the recognition model we supplied the software with 10 good-quality reference “*pchrrr*” calls from each display area obtained at different hours and on different days as training data to capture the extent of natural vocal variation. Following an initial model construction, we adjusted software parameters aiming to achieve a balance between a high recognition rate and a low false-positive rate (Supplementary Table 1).

After running all the recordings through the recognition model, we calculated the number of vocalizations per hour for each display area and then averaged data for all display areas to describe the daily pattern of activity for the population. We also examined the seasonal pattern of activity per display area averaging the number of vocalizations per day, and then examined the population-level pattern averaging data across display areas. All data were corrected for the number of hours sampled per day and per display area.

To describe the vocal repertoire of the Blue-backed Manakin we first identified the calls or songs by listening to recordings and examining spectrograms in Audition 1.5, and then calculated their duration, frequency, rate and number of phrases per call. Spectrograms for graphic display were obtained using Syrinx 2.6 (Burt 2006). The context of usage of each vocalization type was described based on focal observations and videos.

Focal observations, sequences of photos, and videos were used to describe the display behavior of Blue-backed Manakin. The display elements of the dances were described following the terminology of Snow (1963) to allow for comparisons with existing studies on congeneric species.

4. *Reproductive Success at Display areas*

Because this study was conducted only during one mating season and we did not attempt to directly estimate male reproductive success via paternity analyses, we used behavioral data as a proxy for reproductive success. This is justifiable because studies on other species have reported that genetic paternity can be reliably inferred from observed mating behavior (Reynolds et al. 2007). We thus used the number and duration of female visits to a display area during the season, corrected by dividing for the number of hours sampled at each display area, as a proxy of the reproductive success. This display area success is expected to reflect the reproductive success of the alpha male on that area given the extremely low percentage of cases where subordinate males of *Chiroxiphia* are known to mate with visiting females (McDonald 1989b and Duval & Kempenaers 2008). The duration of female visits was calculated by measuring the time elapsed since the shooting of the first photo where a female appeared up until the last photo where it was seen on the perch (hereafter “female visit duration”).

5. *Correlates of Reproductive Success*

We measured 8 different variables to describe male perch attendance and display activity (Table 2). Data were summarized by blocks of ten days to get rid of zeroes and corrected by sampling effort at each display area. Because variables are not independent as most behaviors were part of male displays, many of these variables were correlated to each other. Thus, we used a principal components analysis to reduce our data set to an independent set of variables describing display activity.

To test for relationships between male perch attendance, dance display activity and vocal activity at the display areas with reproductive success, we ran Spearman correlation analyses. To do this we used each principal component obtained from the PCA analysis, rate of vocal activity per day and number of female visits. To determine if there were differences in number of female visits between display areas we ran a Friedman tests and tested whether their distribution deviated from a null (i.e., Poisson) pattern. Variables obtained from photos were transformed using square root to make data more homogeneous, and we report mean values and standard error. All the analysis

were run using SPSS version 22.0 (IBM Corporation, 2013) and graphs built using JMP version 11 (SAS institute, 2013).

Results

1. Activity Patterns at Display areas

a. Display areas and social organization

Display areas consisted of 1-5 males that were consistently seen in the area (Table 3), with ages ranging from 4+ years to 16+ years (see Table 3 for details on the composition of display areas, including status of males). A total of 21 dance perches were found (2-6 per area; Table 3). The timing of finding dance perches was different across display areas; for some areas (Harpia 3) dance perches were found early in the field season (the first week) but for some others (Harpia 7) the main dance perch was only found late in the season (7th week). These perches were live horizontal branches or vines usually within 1m from the ground; perches were typically very clean, without any bark or moss. Within each display area, males displayed mainly on two of these perches where one of the perches was used primarily to practice and the other to display for females. Sometimes, when females were visiting, males moved to other dance perches. Males usually pecked at the display perches to remove leaves, branches, moss or bark.

b. Vocalizations

Male Blue-backed Manakins had a repertoire consisting of at least six different vocalizations, which include invitation calls uttered by lone individuals, duet vocalizations and display vocalizations uttered by two or more males (Fig 5).

The most common vocalization was a “*pchrrr*” with duration ca. 0.32-0.43 secs and frequency range 1.3-2.7 kHz (Fig 5A). Usually the call was uttered during the duet singing by two males, similar to the “*toledos*” reported in Long-tailed Manakin (McDonald 1989a) and to the “*quericos*” reported for Lance-tailed Manakin (DuVal 2007). This call was also uttered by sole males (Primarily alpha males) perched high in their display area, in phrases of 1-7 calls at a rate of 14.4 ± 6.9 calls/minute on average

(SD:6.9). The “*pchrrr*” vocalization also appears to serve the purpose of attracting other males to sing along. Once a beta male joined in, sometimes duet singing started after some “*pchrrr*” calls uttered by the alpha male, but some other times a second invitation call “*cheewee*” was uttered. The “*cheewee*” invitation call had a mean duration of ca. 0.34 (SD:0.4) secs and frequency range 1.7 - 3.4 kHz (Fig 5B). This vocalization was also uttered by males sitting on perches, or by alpha males when betas were absent.

When a duet singing cycle started, males perched very close together and sang synchronized “*pchrrr*” (Fig 5G) at a rate of 40-60 repeats per minute for several minutes. Once a duetting bout had been going on for several minutes, a less common “*wohoo*” call was uttered by any of the males. This call was commonly used when a female arrived or probably as an invitation to move to the dance perch for display given that when one male calls, the other approaches, and then they move together to the dance perch. The call had a mean duration of ca. 0.44 (SD:0.2) secs with a frequency range of 800 hz-1.6 kHz (Fig 5C, 5H).

After both males had come down to the dance perch to display, a “*whee-ee*” was uttered probably to indicate the beginning of the cooperative dance display. The call had a mean duration of ca. 0.40 (SD:0.5) secs with a frequency range between 800hz and 3.8 kHz (Fig 5D).

During the cooperative dance display, a “*wrang*” was uttered constantly by both males while performing coordinated hops or cartwheels. The call had mean duration of ca. 0.70 (SD:0.10) secs and the frequency range was 700 hz-3.7 kHz (Fig 5E). This call was uttered by both males even if there was no female present during the dance display and was similar to the “*nraawnraawnraaw*” reported for Lanced-tail Manakin (DuVal 2007). At higher perches, the call may be given by a single male usually at the hottest hours of the day. Once the alpha male appeared ready for the pre-copulatory display (see below) he uttered a high-pitched “*eeek*” call that signals the beta male to leave the main dance perch. The call has also been reported in Lance-tailed Manakin, and has a mean duration of 0.20 (SD:0.2) secs and frequency range between 3.1 and 8.0 kHz (Fig 5F).

We did not detect any female vocalizations. Mechanical sounds produced by the male wing (Snow 1963) were likely recorded only once, but more detailed observations are needed for a detailed description of these.

c. *Dance displays*

The Blue-backed Manakin dance displays include solo dances and two-male dance displays. A total of 33 two-male dance displays were registered for the season using camera traps (Fig 6). Additionally, from focal observations, we recorded seven two-male dance displays and three single-male dance displays. At no time did we observe any aggressive interactions between males. The duration of the two-male dance display bouts was between 25 and 227.5 secs when no females were present (mean: 118.6 secs, SD: 94.5 secs) and 54.4-330 secs when females were visiting (mean: 164 secs, SD: 102.6 secs). The solo dance displays for females (pre-copulatory display, see below) lasted between 31-133.8 seconds (mean: 69.7 secs, SD: 36 secs). All the mean values have a range of ± 5 secs given the frequency interval between successive photos from the camera traps. Males in definitive adult plumages (alpha and beta males) were the only ones involved in dance displays for females. Gamma males usually practiced the dance displays on secondary dance perches when no females were present. We did not observe more than two males in a coordinated dance display; however, synchronized singing did occur between more than two males.

The dance display consisted mainly of five elements: up-down jumps/ hops, hovering flights, cartwheels or leapfrog dance, back-and-forth hops, and bouncing as described previously by Snow (1963) and Duval (2007; Table 5). In the first part of the two-male dance display, males performed a mix of alternating elements including up-down jumps, hops and hovering flights. Most of the times males kept to their side of the perch, but some times they exchanged sides flying over the female and facing her when they landed. Sometimes males flew to a higher perch and then returned quickly to the dance perch.

The second part of the dance display involved a cartwheel element when males became more coordinated and frenzied. During the cartwheel display males sang the “*wrang*” vocalization continuously and females slid forward on the perch or retreated, but most of the time they remained relatively still (supplementary video 2). When a female moved away from the dance perch, males usually followed her and continued with the cartwheel dancing, seemingly trying to invite her to come back to the dance perch. In

the final jump of the cartwheel element, the alpha male uttered the “*eeek*” call; this call indicates to the beta male to depart from the dance perch, and after this the alpha male continued dancing a solo display or pre-copulatory display. Sometimes, after a short delay, the beta male returned for continued two-male dance display.

Following two-male dance displays and after the “*eeek*” call by the alpha male, the beta male left the dance perch, and the pre-copulatory dance display began. Beta males usually stayed near the dance perch and sometimes uttered “*cheewee*” or “*pchrrr*” calls while the alpha male was performing the pre-copulatory display. The pre-copulatory dance display consisted only of back-and-forth hops and hovering flights followed by bouncing elements executed only by the alpha male in presence on the female and it was silent (see supplementary video 1); the male sometimes flew to a higher perch briefly and returned right away. Females usually followed the back-and-forth hops of the male when excited, and after that, copulation occurred. In some cases when copulation did not occur at the end of the pre-copulatory dance display, the two-male dance display restarted and the precopulatory display was repeated for the same female. Subsequently, the male left the perch and the female usually stayed for a few minutes on the perch during which the female exhibited a extensive preening behavior and then left. Dance displays were also performed in the absence of females by pairs of males and lone males, which probably were practicing.

d. Daily and Seasonal Activity

A total of 377 male visits across all display areas were registered during the breeding season (0.073 mean visits per hour sampled, SD=0.031). Male Blue-backed Manakin were active at dance perches for most of the day, with a peak of activity between 0630 hrs and 1030 hrs (Fig 2A). The range of temperatures for which male/female visits and displays occurred was 22-35 °C with a peak between 26-32°C (Supplementary figure 1). Two-male dance displays and female visits occurred at all hours during the day but were more common between 0630 and 0830hrs, and between 1130 and 1530hrs (Fig 2B). Males were seen taking baths in streams nearby their display areas usually at noon and at the end of the day.

We sampled vocal activity of male Blue-backed Manakins over 9-12 days per display area (Table 1). The recognizer model had a average of total training of 84.02 ±6.78%

(SD), which indicates the percentage of natural variation of the song captured in the model from the training data. This percentage suggests the model is satisfactory because the value exceeds that recommended by the software's designers and is above values typically reported in other studies (Wildlife Acoustics Inc, 2007-2011, Buxton & Jones 2012). The average matching score determined by the recognition model, which indicates the degree of matching between candidate recordings and the recognizer model, was $75.4 \pm 2.1\%$ (SD 2.1) Audio recordings from each display area were run separately, obtaining a general false-positive rate of 5% and a detection rate of 62%. The average matching scores and the detection rate obtained for our data are within the ranges recommended by the software's designers and are similar to those obtained in other studies that used the same software (Wildlife Acoustics Inc, 2007-2011, Agranat 2009).

Using vocal recordings we calculated the daily and seasonal activity of males. Male vocalizations were recorded throughout the day, but we noticed that males usually remained silent when groups of parrots or monkeys were crossing their display areas. Males showed a burst of vocal activity shortly after sunrise in the first hour or two in the morning, and then a second longer peak in the late morning to early afternoon (Fig. 3). Patterns of vocal activity matched those of dance displays and female visits (Fig 2A, Fig 3).

Male activity at perches across the display areas was higher between the third week of January and the third week of February (the first five weeks of monitoring) and dropped significantly thereafter (Fig 4A). Similarly, male vocal activity peaked during the first two weeks of February and dropped significantly thereafter (Fig 4B). The third week of February was very rainy, which may have caused the reproductive season to end early relative to past years when manakins have been studied.

2. Reproductive Success on Display areas

A total of 32 female visits were registered for the season with camera traps (Fig. 6); we recorded 12 additional visits through focal observations which correspond to instances when a dance perch was found for the first time or when replacement of batteries for the camera traps was due so the camera was off. The total number and duration of female visits tended to be higher for the display areas Harpia 3, Harpia 1 and Parahuaco, only

one female visit was reported for the display area Puma and no visits were reported for the display area Harpia 7 (Fig. 7). However, there were no significant differences between display areas for number or duration of female visits (Friedman test: Chi square = 4.4, $p = 0.62$). The distribution of the number of female visits differed from a Poisson distribution but the distribution of the duration of female visits did not ($p=0.01$, $p=0.101$, respectively). From the 32 female visits recorded with the camera traps, we are certain about copulation for only two (photos). This low detection of copulation is probably due to the five-second time-frames used in the configuration of the camera, which did not allow for a continuous record of activity.

3. Correlates of Reproductive Success

The display area Harpia 1 had the highest perch attendance among the display areas (Fig 9), and Harpia 3 and Parahuaco had the highest average duration of single male and two-male dance displays when females were present (Fig 8). The display area with the lowest male vocal activity per hour was Puma with 16 calls per hour, and the area with the highest vocal activity was Harpia 5 with 263 calls per hour (Fig 10B).

Three principal components accounted for the 92.09% of the variance in variables describing perch activity; PC1 explained 61.86% of the variance, PC2 explained 17.33% and PC3 explained 12.88%. PC1 had the highest loadings for number and duration of male visits to the dance perch (Table 4). This component correlated significantly and positively with the number of female visits, indicating that display areas in which perch activity was stronger had greater success in attracting potential mates (Spearman's Rho: 0.502, $p \leq 0.002$; Figure 7a). PC2 had the highest loading for duration of solo and two-male dance displays for females and correlated significantly and positively with the number of female visits (Spearman's Rho: 0.636, $p \leq 0.001$; Figure 7b). PC3 had the highest loading for number and duration of two-male practice dance displays, but this component did not correlate significantly with the number of female visits (PC3, Spearman's Rho: -0.153, $p = 0.375$). No correlation was detected between the variable calls per hour and PC1 (Spearman Rho: -0.071, $p \leq 0.879$). Male vocal activity was also correlated positively and significantly with the duration of female visits (Spearman Rho: 0.786, $p \leq 0.036$) (Fig 10A).

Discussion

1. Activity Patterns at Display areas

Display areas of Blue-backed Manakin in Amazonian Ecuador can be defined as an area containing a group of dance perches dominated by an alpha male, which are also often occupied by one beta male and several gamma males (Gilliard 1959, Snow 1971). At each display area usually two males perform dance displays for females, but the pre-copulatory dance display is performed only by the alpha male; this is similar to observations reported for other *Chiroxiphia* species (McDonald 1989b, DuVal 2007). Alpha males we registered displaying were between 4+ and 16+ years of age. Our finding of a male being still reproductively active at a least 16 years of age is remarkable; this may be the oldest bird reported for the genus *Chiroxiphia* (Duval 2012).

Male Blue-backed Manakins were active most of the day but had a bimodal pattern of perch and vocal activity, with peaks early in the morning and in the afternoon. The peak of perch activity was longer in the morning and shorter in the afternoon, opposite to the pattern of vocal activity that had a shorter peak of activity early in the morning and a more prolonged one in the afternoon. A similar result was documented in an earlier study conducted at the same site based on focal observations (Duraes et al. 2011). Female visits occurred all day but were more common in the afternoon, probably attracted by the peak of male vocal activity and matching/promoting the second peak of perch activity. The peak of perch activity early in the morning may be related to pairs of males or single males practicing dance displays. The daily pattern of male Blue-backed Manakin activity we documented differed from what has been reported for Lance-tailed Manakin (*C. lanceolata*), which has a more homogeneous pattern of activity during the day (DuVal 2007), and for Long-tailed Manakin (*C. linearis*), in which activity extends no further than 15:00 hours (McDonald 1989b).

Some of the differences found between subspecies of *C. pareola* are related to the timing of the main peak of the reproductive season. For *C. p. napensis* in Amazonian Ecuador (this study, Duraes et al. 2011) appears to be between December and February, with the molting season starting in mid- to late March. This differs from the March-June reproductive season reported for *C. p. atlantica* in Trinidad and Tobago (Snow 1963,

1971). This could be related to differences in the pattern of the dry season which is between January and May for Trinidad and Tobago.

We documented a repertoire of at least six different vocalizations for Blue-backed Manakin; this adds two vocalization types to the previously reported repertoire, the “wohoo” and the “whee-ee” (Snow 1963). The vocalization repertoire appears to be more limited than that of Long-tailed and Lance-tailed Manakin, but several elements are shared with these species (e.g., calls for duet singing, two-male dance display and end of two-male dance display). However, as evidenced by comparisons of our sonograms with published sonograms, a notable variation was revealed in the structure of calls between species and subspecies.

Vocal activity differed between display areas. We reported an average vocalization rate of 120 calls per hour which is lower from what has been previously reported (Duraes et al. 2011). This difference could be attributed to the sampling method used by each study and differences in the estimation of the vocalization rate per hour. Duraes et al. (2011) used focal observations and calculated the vocal activity per hour using all the calls and sounds previously reported for the species. In contrast, we used automatic vocalization recorders and only used the display area attendance vocalization “pchrrr” to estimate the vocal activity per hour.

The display behavior of *C. p. napensis* we observed was very similar to what has been reported previously for this species (Snow 1956, 1963, Gilliard 1959). However, it differs from that of other *Chiroxiphia* species. For example, no Pip flights are performed in contrast to Lance-tailed Manakin (DuVal 2007). Butterfly flights are not part of the pre-copulatory dance display but bouncing elements are, which differs from Long-tailed Manakin (McDonald 1989b). Additionally, from comparisons between the videos taken in this study (see supplementary video 2) and videos published for the other species (For Long-tailed Manakin see <http://www.uwyo.edu/dbmcd/lab/lmvideo.htm>; for Lanced-tail Manakin see <http://www.youtube.com/watch?v=cAwevkUaB2Q>), it seems like the dance display of Blue-backed Manakin and Lance-tailed Manakin are more similar in the speed with which the cartwheel or leapfrog dances are executed and differ from the slower Long-tailed Manakin. This difference in the speed of the performance of this elements may be related to the length of the tail, which may limit speed in the Long-tailed Manakin.

2. *Reproductive Success on Display areas*

Although no significant differences were found among display areas in the number/duration of female visits, three of the seven display areas accounted for 73% (Harpia 3, Harpia 1 and Parahuaco) of the total female visits recorded during the field season. If this results in differences in male copulation success, then it can lead to high reproductive skew. The fact that no female visits were registered on display area Harpia 7 is probably a result at least partly of a sampling bias, because we found the main dance perch late in the season. However, the difficulty in finding the main dance perch reflects low male activity at this area.

The Puma display area had the lowest vocalization rate among all the display areas sampled, and also a very low female visitation rate. The low activity and low success of this area could possibly be attributed to the absence of a permanent beta partner; the former beta partner disappeared and we did not find a new bird that could be playing this role (Loiselle unpublished data). This result hints at the importance of the vocal cooperation between alpha-beta males and the consequences of beta loss for the alpha's later reproductive success, given that previous observations indicated that this display area used to be one of the most successful in the population (B. A. Loiselle, unpublished data). Additionally, the fact that the alpha male of this area was 16+ years old may have had an effect on his reproductive success as a consequence of senescence (DuVal 2012).

3. *Correlates of Reproductive Success*

Our data are consistent with the hypothesis that male performance at courtship displays and attendance to display perches is the basis for female choice (Gibson & Bradbury 1985). Number and duration of male perch visits, duration of two-male dance display and duration of the alpha male pre-copulatory display were important variables explaining a display area reproductive success. Our results also support the idea that the cooperative display behavior is important for Blue-backed Manakin to achieve a high reproductive success, given that variables implying cooperation between two males or groups of males, such as duration of two-male display dances and vocal activity, were significantly correlated with the number of female visits (Trainer & McDonald 1995,

Trainer & McDonald 2002, McDonald 1989, DuVal 2007, Ryder et al. 2009a). In addition, as indicated above, the success of the alpha male at a display area lacking a permanent beta partner was low.

The most-visited display areas were also the areas where the average duration of female visits was longer, which could indicate greater copulatory success. In addition, areas with the higher number of associated males also had high female visitation rates, possibly due to them attracting more females by being more noisy when vocalizing in general (Trainer & McDonald 1995, Duraes 2009). High visitation at other display areas may be explainable based on characteristics of males: for example, the alpha male at one of the most highly visited display areas (Harpia 3) was one of the oldest ones (15+ years), with longer tenure; this could translate into greater experience, more coordination between alpha-beta males and possibly a higher rate of revisitation from old females (Ryder et al. 2009, DuVal 2012, 2013). We know very little about female visitation strategies over time (but see DuVal 2013), but old females likely face a tradeoff between (1) receiving a direct benefit by diminishing costs of search, risk of injury or predation by revisiting a male that has been assessed previously, and (2) maximizing the indirect benefits for her offspring by performing a stringent search, following cues and assessing every male at every time (Kokko et al. 2003, Reynolds 1990). The large difference in reproductive success between alpha males of the display areas Puma and Harpia 3 may reflect that there might be more than one year of difference in age between these two males (age calculation reflects a minimum) and also the importance of the cooperation with a beta male. On the other hand, display areas such as Harpia 1 had a high display area attendance which could be explaining the high reproductive success this area had.

Our results provide support for the hypothesis that vocal activity in display areas functions to attract females (Gibson 1996, Duraes et al 2009); areas with higher vocal activity also had higher number of female visits. Previous work on the Long-tailed Manakin proposed that the duration of one element of the dual male display, the butterfly flight, was highly correlated with the copulation rate; however, it was not assessed whether the alpha male performance alone was also important in the copulatory receptivity of the female (McDonald 1989a). The positive correlation between number of female visits and solo male dance display duration for females suggest that in Blue-backed Manakin it is not just the dual male performance during the

displays but also the performance of the alpha male during the precopulatory dance displays what females are using as cues to choose their mate. This further supports the idea that females might be choosing their mates on the basis of subtle differences in motor performance of the alpha males during courtship (Barske et al. 2011).

The extreme specialization of Blue-backed Manakin courtship involving duet singing and cooperative two-male dance displays for females appears to be the result of strong and ongoing sexual selection (Prum 1990). The importance of particular elements in each of those display remain to be tested. We propose that the cartwheels and the jump elements of the two-male dance and that the bouncing element of the solo precopulatory display may be the most important cues of a male's vigor (Darwin 1871) because they seem to require higher motor skills and more energy to be performed (Barske et al. 2011). Other determinants of male success may be important in this system as in other manakin species, including plumage brightness (Doucet & Montgomerie 2003, Stein & Uy 2005), territory location (Shorey 2002, Fiske et al. 1998), amount of sunlight hitting the dance perch (Heindl & Winkle 2003), genes (Duraes 2009, Ryder et al. 2009b), song performance (Trainer & McDonald 1993), parasite load (Hamilton & Zuk 1982), or lek size (Fiske et al. 1998).

In sum, this study suggests that male quality influences female mate choice in Blue-backed Manakin; female mate choice is influenced by male perch attendance, male vocal activity and male display activity. As described above, the 'good genes' hypothesis poses that variation in mate choice among females should be low because all females would choose the better-quality individuals of a population, resulting in high reproductive skew. Such a pattern could be especially marked if females cue on behavioral traits that signal male vigor. We found that in the Blue-backed Manakin, behaviors signaling vigor such as perch attendance, dance display duration for females and vocal activity are central elements for female mate choice. Perch attendance, dancing and singing displays have been considered as honest indicators of male vigor and quality (Byers et al 2010); our results showing that females preferred males that attended and displayed at a higher rate may thus suggest they are selecting better quality males and probably getting the indirect benefit of 'good genes' for their offspring. However, we can not rule out a 'runaway' mechanism for female mate choice.

Finally, we note the value of using automated data-recording devices for field studies of behavior. We realize that the time frame of our study was short and that the number of display areas studied was small, and thus that our conclusions should be taken with caution. However, our implementation of automated data collection techniques allowed for an intense sampling effort that might compensate for those restrictions. Also the usage of these techniques may alleviate any bias that may be produced by the effect of different observers collecting data and minimize the number of man hours in the field while maximizing the amount of data collected simultaneously.

Figures and Tables

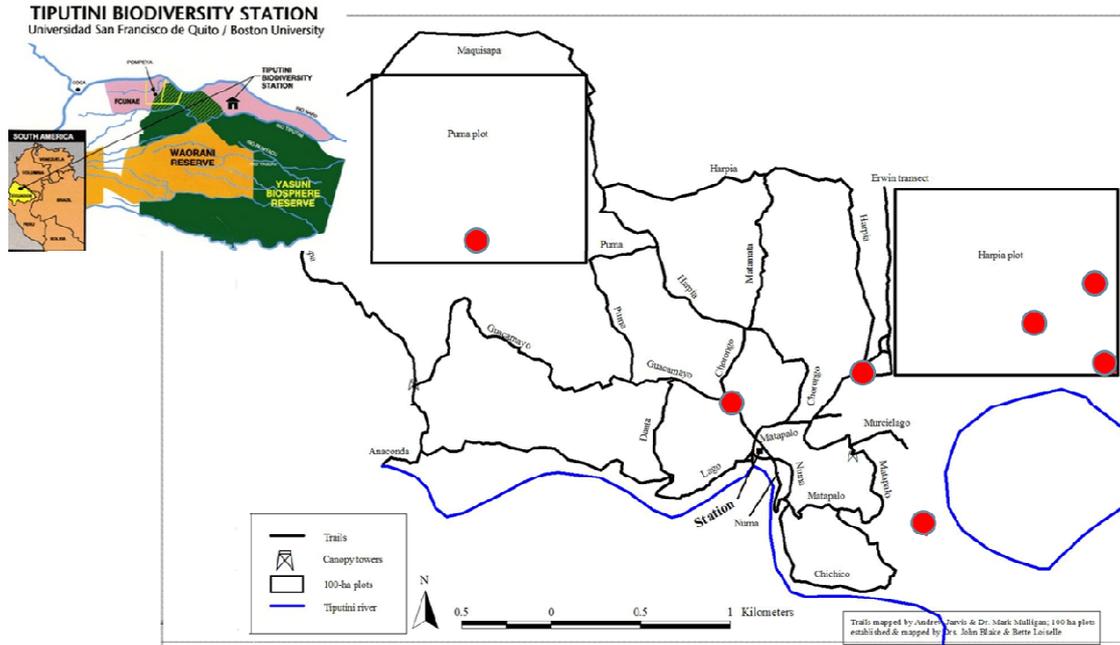


Figure 1. Map of Tiputini Biodiversity Station in eastern Ecuador, where field work was conducted. Red dots indicate the location for each of the seven display areas studied (Trails mapped by Andrew Jarvis & Mark Mulligan; 100ha plots established and mapped by John Blake & Bette Loiselle).

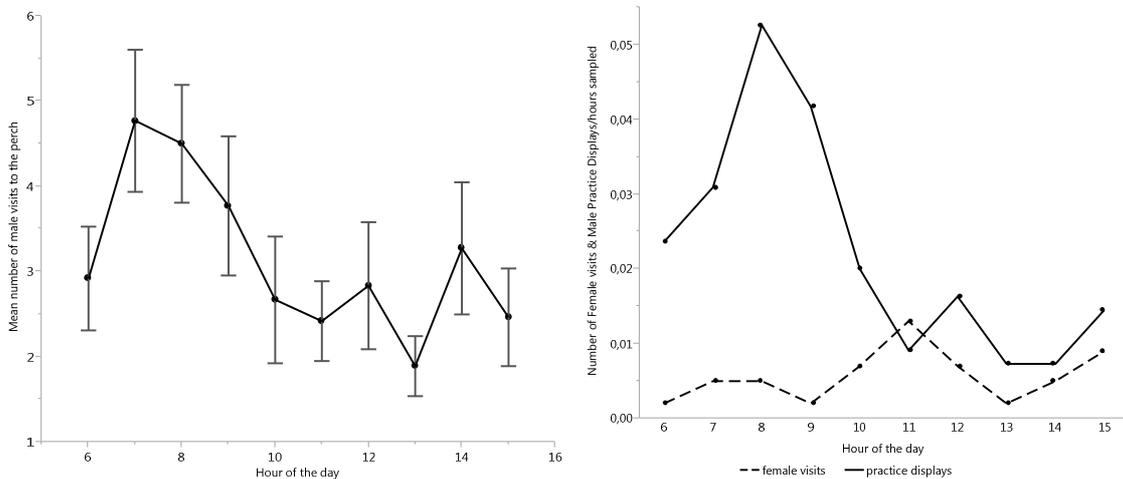


Figure 2. Male and female Blue-backed Manakin daily activity from 0600-1600 hours. (A) shows averages across the display areas of male perch visits per hour of the day for the season; the graph shows a peak of activity in male perch attendance early in the morning and then a short peak in the afternoon. Bars represent standard error, sample size 380 (B) shows total number of female visits and total number of male practice displays per hour of the day corrected by number of hours sampled at each hour of the day across all display areas (~500 hours per hour of the day). The graph shows a

bimodal pattern of activity for male practice dance display. Female visits 32, male practice displays 123.

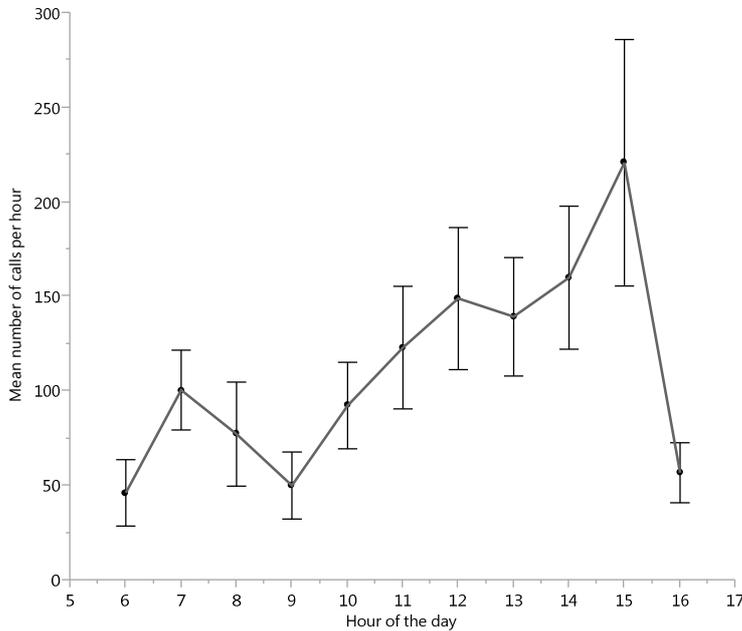


Figure 3. Male Blue-backed Manakin daily vocal activity. The graph shows a bimodal pattern of vocal activity with a more sustained peak in the afternoon. Data were averaged over all display areas and represent mean “*pchrrr*” calls per hour standardized by the number of hours sampled at each hour of the day. Bars represent standard error. Sample size 72

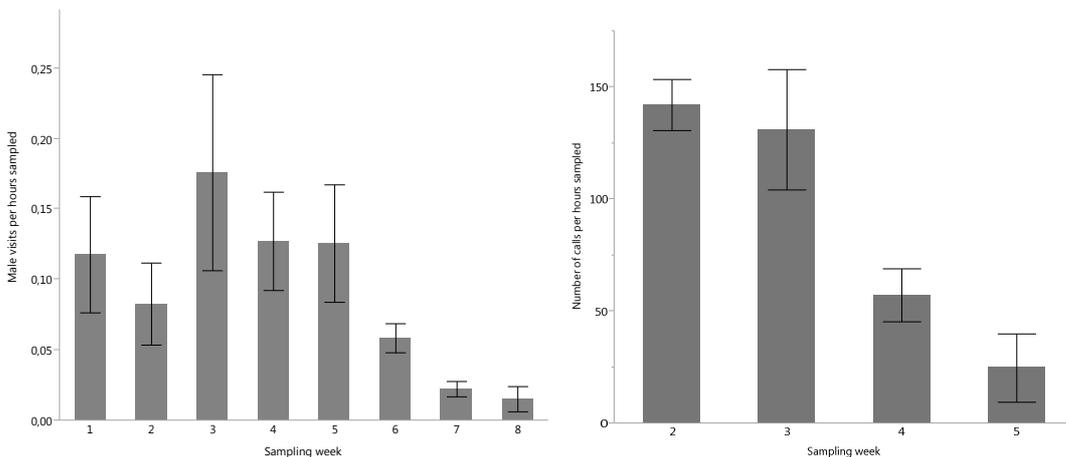


Figure 4. (A) Male Blue-backed Manakin perch activity for the season, the figure shows a higher perch activity between the first and the fifth week of sampling. (B) Male Blue-backed Manakin vocal activity for the season, the figure shows a higher vocal activity between the second and third week of sampling. Week number 1 represents the last week of January and week number 8 represents the third week of March. Data were averaged over all the display areas and represent mean values of (A) number of perch

visits/hour recorded with camera traps and (B) number of calls per hour recorded with Songmeters. Error bars represent the standard error. Sample size for A: 380, B: 720.

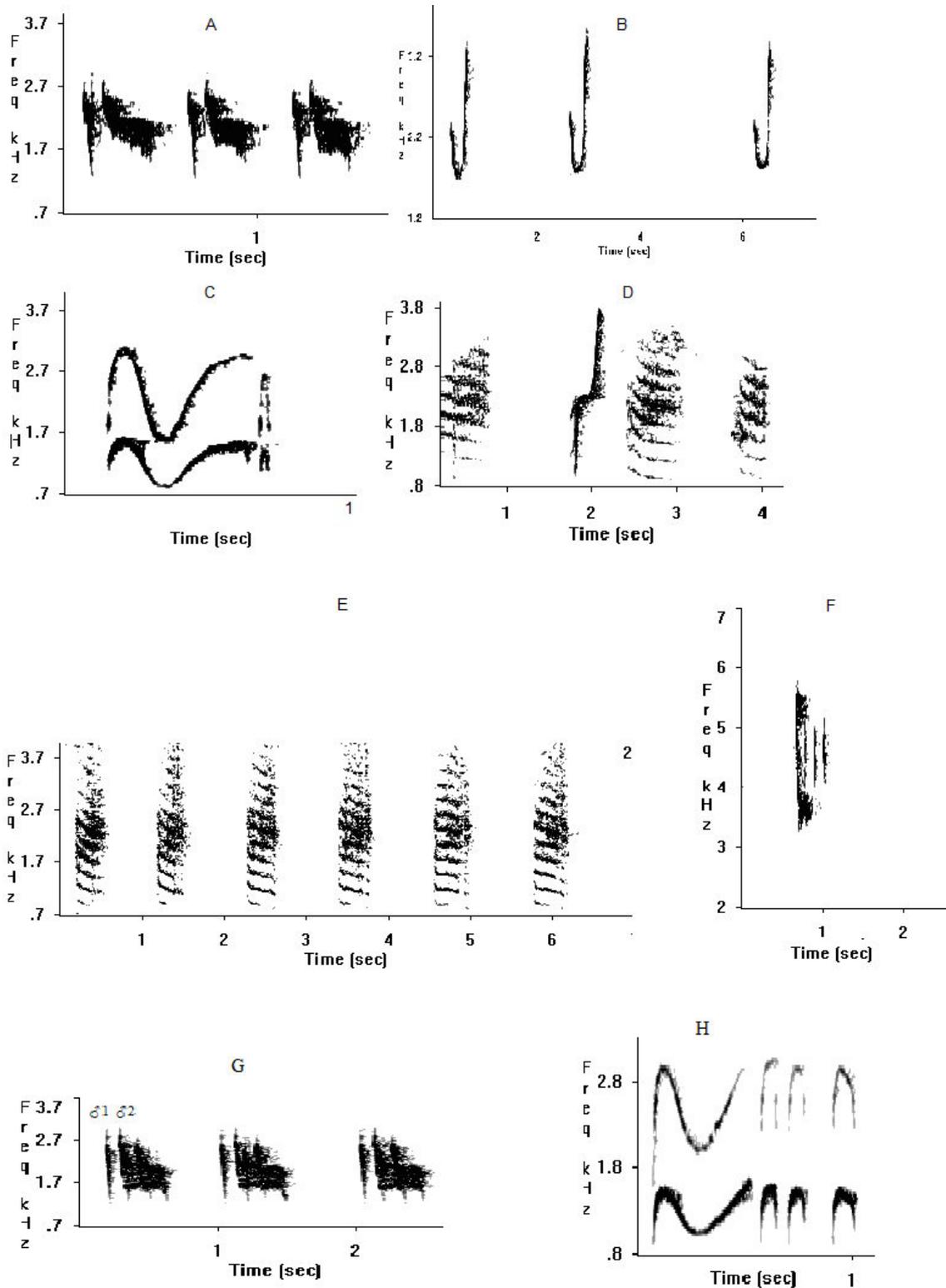


Figure 5. Sonograms for the six vocalizations given by Blue-backed Manakin. A: “pchrr” call given usually by the alpha male and uttered in the duet call bouts, B: “cheewee” invitation call given to start a duet call bout, C: “wohoo” invitation call given

to move to a dance perch, D: “*whee-ee*” call given in the beginning on a two-male dance bout, E: “*wrang*” call given during the cartwheel element of the dance display, F: “*eeek*” call uttered usually by the alpha male at the end of a two-male dance bout indicating to the beta male to go away, G: duet singing, H: calls that some times accompany the “*wohoo*” call.

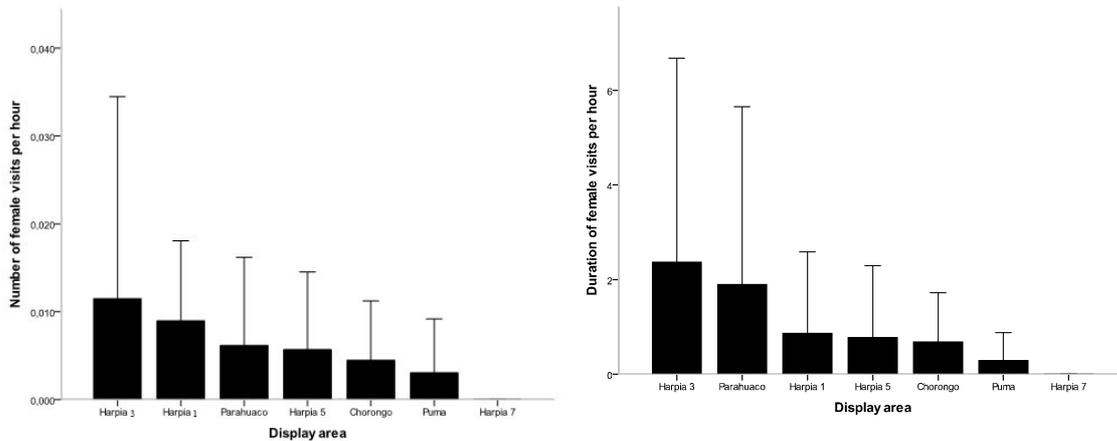


Figure 6. (A) Number of independent female visits per hours sampled between display areas for the season. (B) Duration of female visits (seconds) per hours sampled on manakin display areas. Areas Harpia 1 and Harpia 3 had the highest number of female visits and Harpia 3 and Parahuaco had the longest female visits. Data represent visits registered with camera traps and are shown as mean values for the blocks of ten days of data as data were summarized and bars represent standard error. No females visited Harpia 7, so this area does not have a bar.

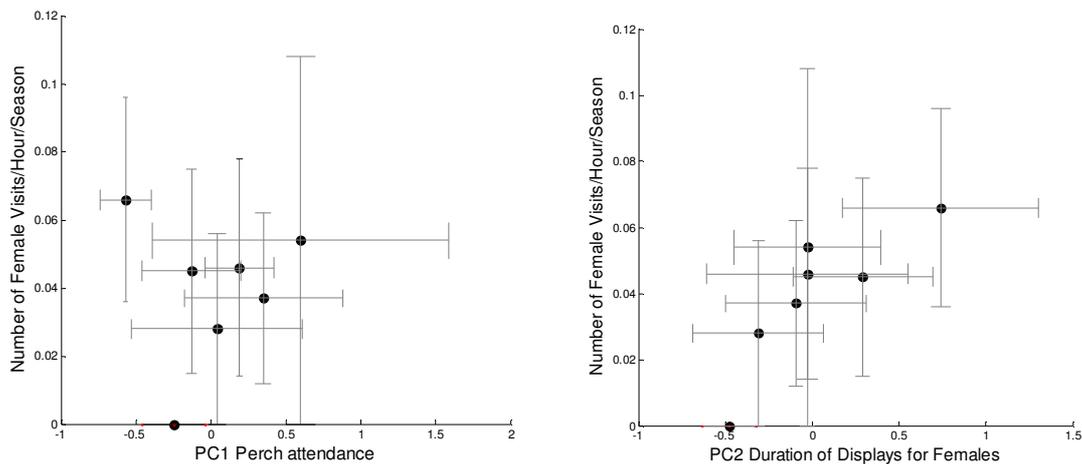


Figure 7. (A) A positive and significant correlation between male number and duration of perch visits (PCA1) and number of female visits is depicted. (B) A positive and significant correlation between male duration solo male and two-male dance displays for females (PCA2) and number of female visits is depicted. Data were summarized by season and points represent mean values. All data were corrected for sampling effort.

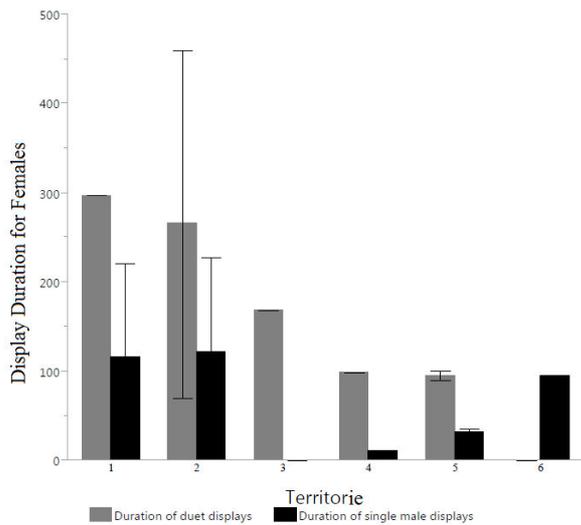


Figure 8. Average duration of solo (grey bars) and two-male (black bars) dance displays between display areas for the season in seconds. Solo and two-male dance displays were on average longer in areas Harpia 3 (1) and Parahuaco (2). Data are shown as a mean values and bars represent the standard error.

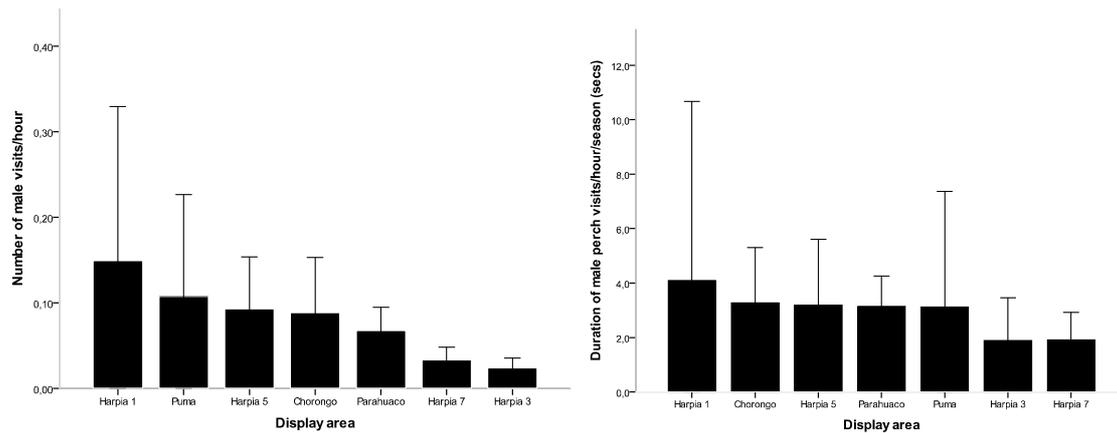


Figure 9. (A) Average number and (B) duration of male perch visits between display areas for the season. Display area Harpia 1 had the highest perch attendance of all areas. Data are shown as a mean values and bars represent the standard error.

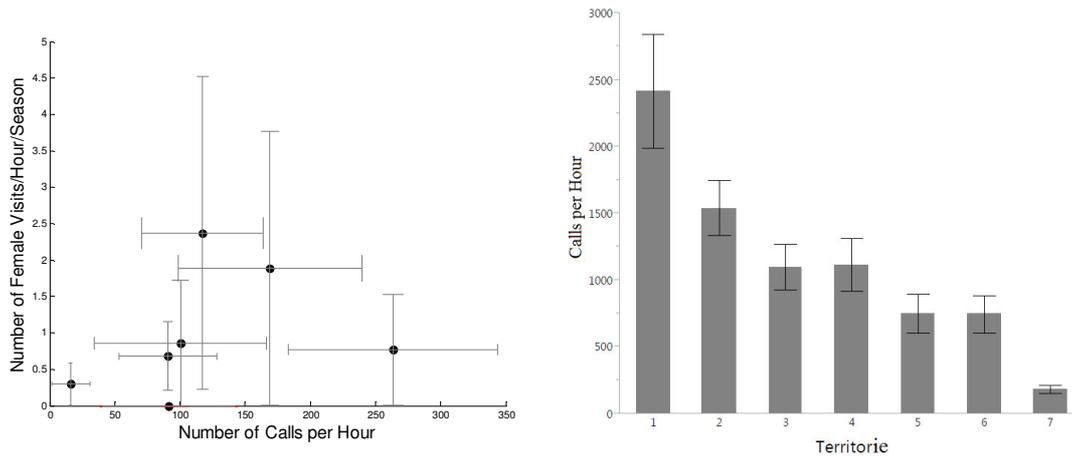


Figure 10. (A) Call rate by male manakins is positively correlated with the Average duration of female visits to dance perches in periods of ten days. (B) Display areas vocal activity for the season. Areas Harpia 5 (1) and Parahuaco (2) had the highest rate of vocal activity. Data are shown as a mean values for all the days sampled in the season.

Table 1. Camera traps and Songmeters sampling effort at Tiputini Biodiversity Station. The number of days sampled overall, the number of days sampled where birds were recorded on the dance perch, and total number of hours cameras were deployed are provided. In addition, the total number of photos with records of manakins on the dance perch are provided for each display area.

Display Area	Sampling dates	Days sampled for vocal activity	Days sampled for perch activity	Days sampled with photos with records	Camera hours	Number of photos with records
Chorongo	21 Jan-18 March	9	55	30	820.8	2154
Harpia 7	21 Jan-17 March	12	53	23	738.0	615
Harpia 3	21 Jan-18 March	11	54	18	813.0	881
Harpia 1	4 Feb-18 March	11	38	20	488.0	2303
Harpia 5	30 Jan-18 March	10	46	26	1083.0	2947
Parahuaco	01 Feb- 18 March	10	46	34	968.5	1906
Puma	28 Jan-18 March	12	39	20	418.5	1030

Table 2. Description of the behavioral variables used to compare males among display areas (independent variables) and predict aspects of female visits (dependent variables).

Variable	Definition
<i>Independent</i>	
Number of male visits	Number of male visits to the dance perch for purposes other than displaying
Duration of male visits	Duration of male visits to the dance perch for purposes other than displaying
Number of two-male dance practicing displays	Number of displays executed between alpha, beta or gamma males without the presence of a female
Duration of two-male dance practicing displays	Duration of displays executed between alpha, beta or gamma males without the presence of a female
Duration of alpha-beta displays	Duration of displays executed between alpha-beta males in the presence of a female
Number of solo practicing displays	Number of displays executed by a single male (alpha, beta or gamma) without the presence of a female
Duration of solo practicing displays	Duration of displays executed by a single male (alpha, beta or gamma) without the presence of a female
Duration of alpha solo displays	Duration of the solo (pre-copulatory) displays executed by the alpha male in presence of a female
<i>Dependent</i>	
Number of female visits	Total number of female visits to a display area for the season
Duration of female visits	Total duration of female visits to a display area for the season

Table 3. Characteristics of the number of dance perches and males found on the seven Blue-backed Manakin display areas.

Display area	Number of dance perches found	No of males at the area	No of Alpha, Beta and Gamma males	Alpha male min age
Chorongo	2	3	1,1,1	8+
Harpia 1	2	2	1,1,0	4+
Harpia 3	3	2	1,1,0	15+
Harpia 5	6	5	1,1,3	12+
Harpia 7	2	2	1,1,0	8+
Parahuaco	4	4	1,1,2	5+
Puma	2	1	1,0,0	16+

Table 4. Component loadings of behavioral variables as quantified by principal components analysis (n=36). PC1 generally was characterized by male perch attendance, PC2 was characterized by performance during the two-male and solo male dance displays for females and PC3 was characterized by number and duration of two-male practice dance bouts. In bold are highlighted the highest loadings for each PC.

Trait	PC1	PC2	PC3
Number of male perch visits	0.898	-0.108	-0.243
Duration of male perch visits	0.919	0.049	-0.238
Number solo male displays without females	0.817	-0.397	-0.308
Duration solo male displays without females	0.853	-0.357	-0.230
Number two-male displays without females	0.754	-0.145	0.614
Duration of two-male displays without females	0.755	-0.114	0.622
Duration solo male displays for female visits	0.689	0.646	-0.032
Duration of two-male displays for female visits	0.539	0.798	-0.048

Table 5. elements and sequences of the two-male and solo male (pre-copulatory) dance displays. A complete courtship display is a combination of several elements and includes repetition of elements in a consistent way.

Display	Elements
<i>Two-male dance display</i>	Up-down jumps Up-down hops Hovering flights Flights to higher perches Cartwheels "Eek"
<i>Solo (pre-copulatory) dance display</i>	Back-and-forth hops Bouncing Hovering flights Copulate

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Supplementary Material

Table 1. Parameters used in the software to create the recognizer pattern.

Parameter	Adjustment
Sample rate	22050 Hz
FFT size	512
FFT overlap	½
Frequency minimum	990 Hz
Frequency range	3800 Hz
Background filter	1second
Maximum syllable	1milisecond
Maximum syllable gap	12 milliseconds
Maximum song duration	700 milliseconds
Dynamic range	25dB
File minimum quality	20 %
Minimum matching score	50 %

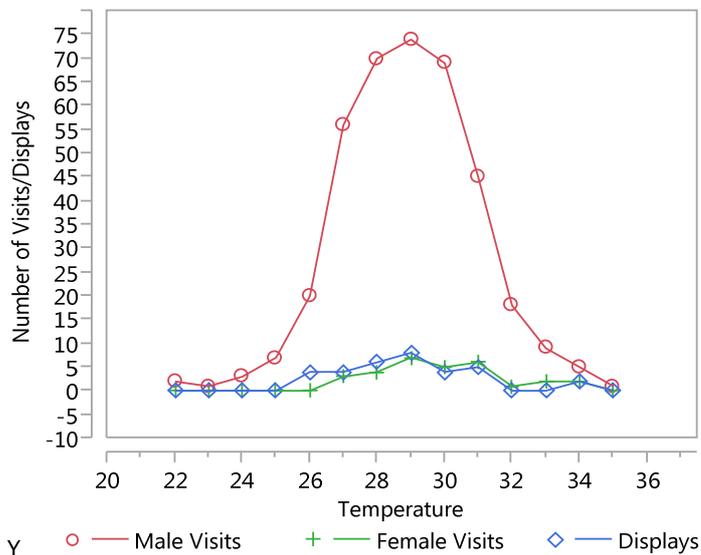


Figure 1. Blue-backed Manakin temperature activity.

Video 1

One male practicing the solo dance display

<http://www.youtube.com/watch?v=c8fbVdzz5WE>

Video 2

Two-male dance display for a female

<http://www.youtube.com/watch?v=-XvPKTj-9hs>